



Perspective

Biodiversity-rich European grasslands: Ancient, forgotten ecosystems

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ABSTRACT

Worldwide reforestation has been recommended as a landscape restoration strategy to mitigate climate change in areas where the climate can sustain forest. This approach may threaten grassland ecosystems of unique biodiversity as such policies are based on the false assumption that most grasslands are man-made. Here, we use multiple lines of evidence (palaeoecological, pedological, phylogenetic, palaeontological) from Central Eastern Europe and show that various types of grasslands have persisted in this area throughout the postglacial i.e., the past 11,700 years. A warm and dry climate, frequent fires, herbivore pressure and early Neolithic settlements kept forests open until widespread forest clearance beginning 4000 to 3000 years ago. Closed forest cover has been the exception for the last two million years. This long-term persistence has likely contributed to the high biodiversity of these grasslands. Consequently, we call for a more cautious prioritisation of the protection of what may be erroneously considered natural, i.e. forests, by many environmental specialists and managers. Instead we provide a new framework for a better understanding of the evolution and persistence of different grassland types and their biodiversity, so that grasslands can be better understood, valued and conserved.

1. Introduction

The World Resources Institute (WRI) Atlas of Forest and Landscape Restoration was designed to identify opportunities for landscape restoration worldwide, an initiative supported by several international organisations concerned with land degradation, climate change mitigation and biodiversity loss (<http://www.wri.org/applications/maps/flr-atlas>). It contrasts the potential extent of tree cover based on climate conditions with the current distribution of forest globally. This map identifies 23 million km² of land worldwide suitable for tree planting, mostly being currently open landscapes with grassland (<http://www.wri.org/applications/maps/flr-atlas>). However, grassland experts oppose the offsetting of agricultural deforestation through the afforestation of grassy ecosystems arguing that this approach ignores the unique biodiversity, cultural significance and important ecosystem services provided by this ecosystem (Willis et al., 2008; Parr et al., 2014; Veldman et al., 2015a,b; Bond, 2016; Joshi et al., 2018). Their imperative is to map “old-growth” grasslands, where tree cover is naturally sparse and where such afforestation would be detrimental.

Another important debate is how to provide strategies to reduce the impact of the ongoing abandonment of high biodiversity grasslands, therefore preventing succession towards low biodiversity secondary shrub and forest communities (Biró et al., 2018; Valkó et al., 2018a).

Here we go further and challenge the perception that treeless areas in temperate regions, where the current climate would permit forest development, have all previously been forested and therefore grasslands and open canopy woodlands are secondary habitat types in these regions. This perception fails to consider the vital role of natural disturbances such as fire or herbivores (Bond and Keeley, 2005). We illustrate this by analysing evidence from Central Eastern Europe. The choice of this region is based on the following arguments: i) it hosts one of the largest tracts of grasslands in Europe crucial for maintaining biodiversity in European agricultural landscapes (Wilson et al., 2012); ii) it has one of the highest small-scale species diversities in the world (Dengler et al., 2014; Turtureanu et al., 2014; Chytrý et al., 2015); and iii) it is a transitional, complex region between closed forest and steppe biomes (Bohn et al., 2004) and hence contains grasslands of diverse origin and history. Yet, despite these features, grasslands are rarely

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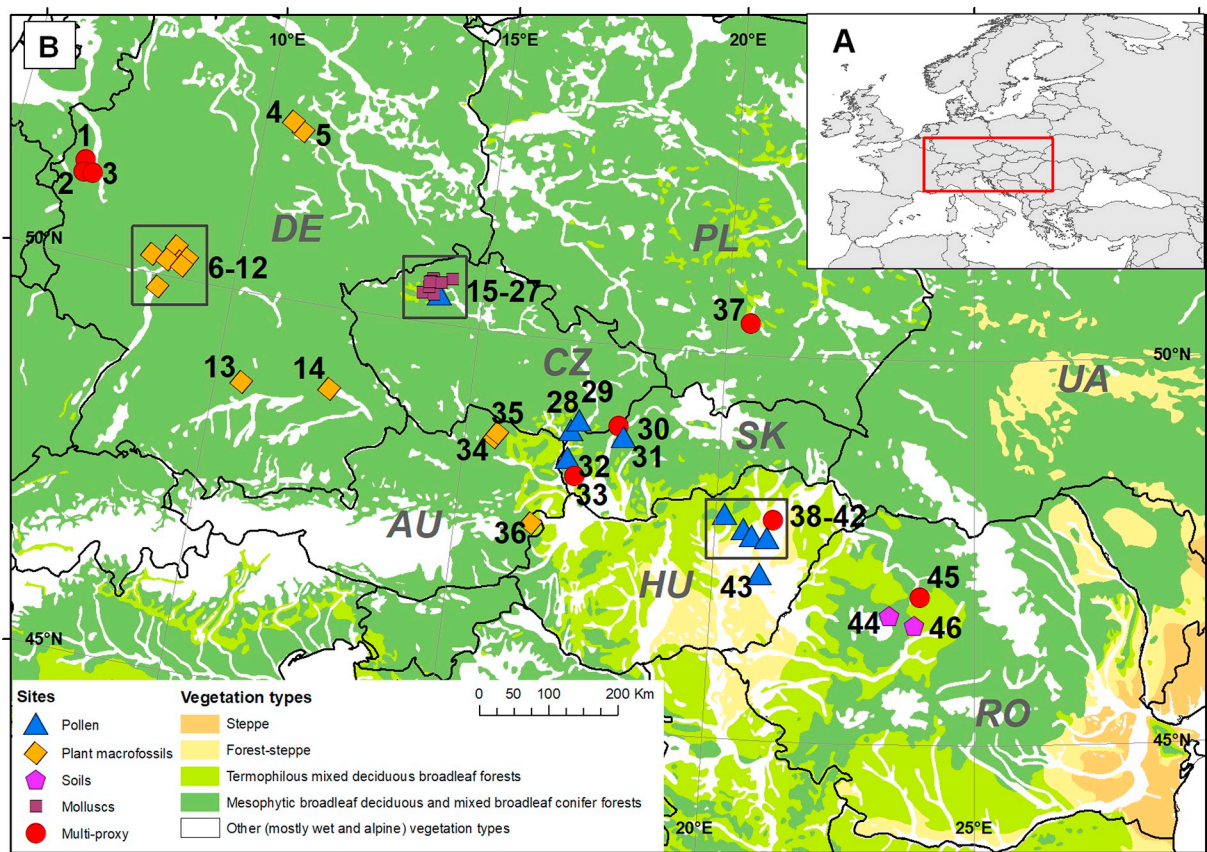


Fig. 1. Location of the study area in Europe (A) and the distribution of the main vegetation types in Central Eastern Europe based on the potential natural vegetation map of Europe (B). Colour symbols show location of various types of fossil records extracted from literature (Table 2 and S1) indicating either continuous grassland presence throughout the Holocene or during the afforestation phases of the mid Holocene (9000–4000 cal yr BP). These fossil records reveal that grasslands were continuously present throughout the Holocene in places where potential natural vegetation has been assumed to be forest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highlighted as biodiversity hotspots. This is because the key characteristics and ecological processes important for this classification, such as biodiversity intactness and a lack of human disturbance, cannot be readily applied to them (Mittermeier et al., 2011). Our goal is to better define grassland types based on their origin, age and the drivers of their formation and maintenance so that grasslands can be better understood, valued and conserved.

2. A new framework for defining European grassland types

Bohn et al. (2004) provided a geobotanical expert assessment, which maps Europe's potential natural vegetation (PNV) i.e., the vegetation cover that would exist today in the absence of human activity. It defines most areas that are currently covered by grasslands or open woodlands in Central Eastern Europe as dominated by deciduous broadleaved forest or mixed coniferous and broadleaved forest (Fig. 1). Open, or at least partly open vegetation types, are only recognised in the lowlands of the Carpathian Basin. Fossil records show that grasslands and open canopy woodlands covered extensive areas in Central Eastern Europe during the Pleistocene (i.e., the past 2 million years) when cold and dry climate conditions prevailed (Kuneš et al., 2008; Ellenberg and Leuschner, 2010; Feurdean et al., 2014; Magyari et al., 2014). Warmer climate conditions during the Holocene (i.e., the last 11,700 years) then greatly reduced the potential distribution and/or extension of grasslands (Birks and Willis, 2008). An especially critical period for grassland persistence was the mid Holocene period (9000–4500 cal yr BP), when moister climatic conditions triggered forest expansion (Roberts et al., 2018). Identification of warm/moist

stage refugia for grasslands (i.e., locations where they persisted) during the mid Holocene is therefore of crucial importance for understanding ancient grasslands.

It is widely accepted that natural grasslands growing on rocky skeletal and other poor soils with a permanent or seasonal moisture deficit i.e., outcrops, steeper slopes, gravel riverbanks, salt and sandy soils the so-called primary grasslands have survived continuously in small pockets throughout the Holocene in their current locations (Lang, 1994; Poschlod and Wallis de Vries, 2012). Currently, the extent of these grassland types is limited, apart from grasslands growing on salt and dry sandy soils, which are more common in the Carpathian Basin (Molnár and Borhidi, 2003; Deák et al., 2014). It is therefore highly improbable that these small, isolated grassland areas were the only refugia of the extraordinarily rich grassland flora of so-called “semi-natural” grasslands. The high genetic diversity of some grassland plant species in this region (Turtureanu et al., 2014) and the remarkable species richness and endemic plant and animal species typical for grasslands (Chytrý et al., 2015) suggest a wider extent of primary grasslands during the Holocene.

In contrast to the primary grasslands, open canopy woodlands and grasslands currently found in areas where climate and soils would allow forest growth, and which are only extensively managed (i.e., no artificial fertiliser and pesticide application) are considered to be semi-natural (Pärtel et al., 2005; Leuschner and Ellenberg, 2017). Here, we challenge the view that most of these grasslands have replaced formerly naturally occurring forests within recent centuries or millennia. We present multiple lines of evidence (palaeobotanical, pedological, phylogenetic, palaeontological) from five countries in Central Eastern

Table 1
Species-rich grassland types.

| Grassland type | Characteristics |
|------------------------|--|
| Primary grassland I | Natural grasslands on skeletal and other poor soils with moisture deficit |
| Primary grassland II | Ancient grasslands formed and maintained mainly by climate conditions and natural fires, herbivores and, later, also influenced by anthropogenic disturbances |
| Semi-natural grassland | Secondary grasslands formed and maintained by anthropogenic disturbances (deforestation, livestock grazing, cultivation, use of fire) in areas suitable for forests during the late Holocene |

Europe, a region with some of the highest-biodiversity grasslands of the world. Firstly, we review published direct records of past grassland occurrence (pollen, plant macrofossils, charcoal) from both natural (lakes, bogs) and archaeological archives, alongside other indirect fossil (pedological, zoological) and recent genetic evidence from Central Eastern Europe. Secondly, we review the characteristics of the environmental and disturbance factors (climate, fire, herbivores and human impact) during the Holocene in this region. Finally, we evaluate whether continuous grassland presence was possible under the

Holocene climatic conditions, fire and grazing regimes, and increasing anthropogenic impacts.

Based on their age and the drivers of their formation, we set out a new framework for three types of grasslands in Central Eastern Europe: 1) Primary, natural grasslands on skeletal and other poor soils, which have existed throughout the Holocene until the present; 2) Primary, ancient grasslands on deeper soils, maintained by climate and disturbances during the early Holocene and then predominantly by disturbances until the present; and 3) Semi-natural grasslands, extensively managed grasslands, formed and maintained by anthropogenic disturbances during the late Holocene (Table 1). We argue for the recognition of the importance of previously overlooked ancient grasslands that have persisted throughout the Holocene, maintained by natural and later also by anthropogenic disturbances.

3. Multi-proxy evidence for grassland persistence during the Holocene

3.1. Fossil plant evidence

Pollen and palaeobotanical records from natural archives (lakes and peatbogs) in currently grassland-rich areas in Central Eastern Europe indicate the prevalence of a more open landscape between 11,700 and

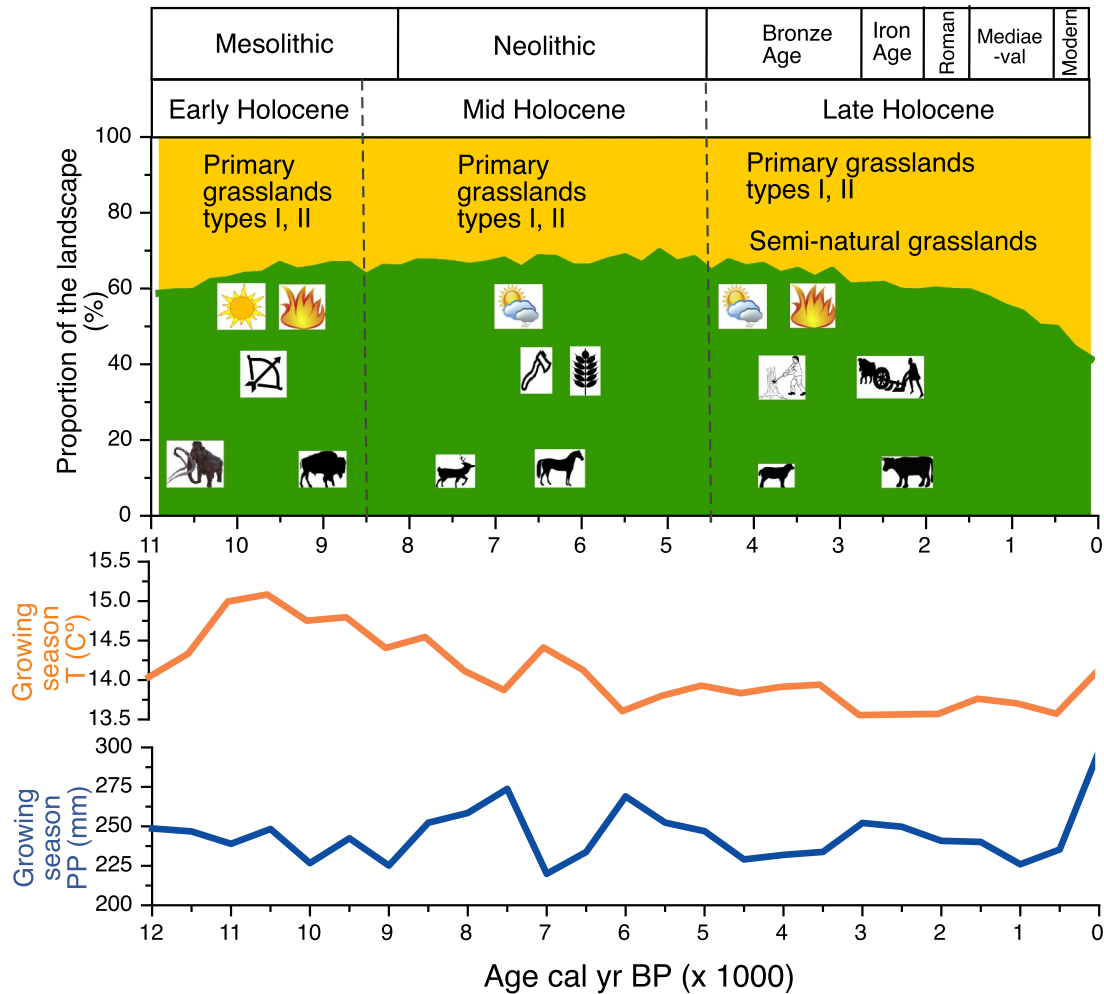


Fig. 2. Pollen based reconstruction of forest (green) versus open land cover (yellow) from Central Eastern Europe during the Holocene using the pseudobiomisation method (Fyfe et al., 2015). Cumulative land cover record was constructed by spatially aggregating 96 pollen records extracted from the Pangaea Database and distributed across the region shown in Figs. 1 and S1. Forest cover includes both broadleaf and conifer trees, whereas open land cover includes pastures/natural grasslands, and arable/disturbed land. Geological and archaeological periods as well as the predominance of each grassland type throughout the Holocene are also highlighted. Trends in simulated growing season temperature and precipitation for Lake Stiucii after Feurdean et al. (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

9000 cal yr BP and the maximum extent of forest cover between 9000 and 4500 cal yr BP (Figs. 1, 2; Table 2, Fig. S1). While these studies show a reduction in grassland cover, especially of xerothermic and floodplain grasslands during the mid Holocene, there is no evidence of their widespread disappearance. Rather, there is strong support for their persistence, given the concurrent presence of many grasslands and light-demanding tree and shrub taxa i.e., *Adonis* spp., *Artemisia* spp., *Centaurea* spp., *Festuca rubra*, *Festuca* spp., *Filipendula* spp., *Helianthemum* spp., *Potentilla erecta*, *Potentilla* spp., *Sanguisorba* spp., *Trifolium* spp., *Thymus* spp., during this period (Fig. 1; Table 2). Archaeobotanical reports from Hungary and Poland suggest an even greater proportion of heliophilous taxa growing locally than pollen records indicate (Fig. 1; Table 2). Remains of grassland species including steppe elements i.e. *Asperula cynanchica*, *Phleum pratense*, *Plantago media*, *Stipa pennata*, *Stipa* sp., *Silene vulgaris*, *Teucrium chamaedrys*, have been reported from archaeobotanical records of early Neolithic sites from Germany (Fig. 1; Table 2) and Czech Republic (Archaeobotanical Database of the Czech Republic; <http://www.arup.cas.cz>). Calcareous grasslands have also been identified at Neolithic lakeshore sites in the northern foothill of the Alps (Fig. 1; Table 2). The species found are typical of closed xerophilous and mesophilous grasslands at sites where trees would have been able to grow under the climatic conditions of the mid Holocene. Taken together, fossil plant evidence from natural archives and archaeological sources suggest that grasslands existed locally before the start of the Neolithic and therefore before marked human impacts. These findings also demonstrate grassland persistence throughout the mid Holocene, although archaeological records show the occurrence of higher grassland diversity than that found in pollen records.

3.2. Zoological evidence

Indirect evidence for the persistence of open, or partly open landscapes throughout the mid Holocene comes from the palaeontological remains of animal species restricted to extensive, open habitats (Fig. 1). Results from the Carpathian Basin (Hungary and Romania) show that several species typical of steppic environments e.g., *Asinus hydruntinus* (European Wild Ass), *Equus ferus* subsp. *gmelini* (Eastern European Wild Horse), *Microtus gregalis* (Narrow Headed Vole), *Ochotona pusilla* (Steppe Pika), *Otis tarda* (Great Bustard) and *Vipera ursinii* subsp. *ra-kosiensis* (Meadow Adder) were abundant during the early Holocene (Németh et al., 2017). They became discontinuously present from 8000 cal yr BP and several of these species disappeared between 5000 and 4000 cal yr BP at a time of increased anthropogenic pressure, but in a grassland landscape. Fossil malacological records in currently grassland-rich landscapes reveal a similar picture (Fig. 1); a continuous Holocene presence of strictly open habitat molluscs (*Chondrula tridens*, *Helicopsis striata*, and *Vallonia pulchella*) unable to survive in closed forests (Ložek, 2007; Horsak et al., 2009; Moskal del Hoyo et al., 2018). Overall, while there is evidence that many open habitat mollusc species contracted their range during mid Holocene forest expansion, there is also robust support for their local long-term persistence and consequently also for the continuity of grassy ecosystems.

3.3. Phylogeographic evidence

Phylogeographic analysis represents a further source of data facilitating the interpretation of the distribution of past grasslands. A pattern of genetic diversity decline from core populations in southern Siberia towards the range periphery of smaller populations in western Europe has been confirmed for several grassland plant species including *Adonis vernalis* (Hirsch et al., 2015), *Iris aphylla* (Wroblewska, 2008), *Stipa capillata* (Wagner et al., 2011) and *Stipa pennata* (Wagner et al., 2012). These studies have also revealed a surprisingly low genetic differentiation between central and peripheral intermediate populations, or a complete lack of private alleles among peripheral

populations (e.g. Wagner et al., 2012; Hirsch et al., 2015), which may reflect the absence of any long-standing isolation of these populations. This implies that these species must have had a more continuous past distribution in Central and Eastern Europe allowing gene flow and interbreeding. Rapid progress in the field of DNA analysis, especially environmental DNA, may shed further light on the origin and past range distribution of grasslands (Thomsen and Willerslev, 2015).

3.4. Pedological evidence

A further line of evidence used in the interpretation of former vegetation distributions comes from soil types (IUSS Working Group WRB, 2007). In Central Eastern Europe, dark soils (chernozems) from steppe and forest steppe zones are considered to have developed before the spread of forests and to have persisted under open or semi-open vegetation (Pokorný et al., 2015). Others, however, view these soils as having survived under forest development (Eckmeier et al., 2007). A palaeo-pedological analysis from the Transylvanian Basin (Romania) shows the occurrence of islands of dark soils of Pleistocene age (20,000–14,000 cal yr BP), which, in drier areas, persisted until the present (Pendea et al., 2002) suggesting grassland persistence throughout the Holocene. However, in other areas of the Transylvanian Basin, dark soils were overlain by Luvisols, typical of nemoral forests, about 5000 cal yr BP (Timar Gabor et al., 2010) when wetter climatic conditions prevailed, whilst the current vegetation is predominantly grassland. Grassland occurrence on soils typically favouring forests may be explained by the prevalence of open woodlands throughout the Holocene, allowing the long-term persistence of dark soil, rather than the post-deforestation formation of this soil type. Forest soils occur extremely rarely on chernozems developed on loess substrates in the Hungarian Plain therefore suggesting the long-term existence of steppe grasslands (Máté, 1957; Molnár et al., 2012). Indeed, the continuous dominance of grasslands from the Late Pleistocene on loess deposits in the southern Carpathian Basin has been demonstrated on the basis of *n*-alkane biomarkers (Marković et al., 2018). Thus, pedological evidence from chernozems, including those developed on loess, shows that chernozems existed under open or semi-open vegetation.

4. Drivers of grassland persistence during the Holocene

4.1. Climate conditions

Proxy-based and climate simulations indicate warmer-than-present summer temperatures, lower precipitation and soil moisture, and greater seasonality in the early Holocene (11700–9000 cal yr BP) in Central and Eastern Europe at the time of maximum grassland extent (Feurdean et al., 2013, 2014; Heiri et al., 2015). Palaeoclimatological records show a decline in temperatures in this region from approximately 9000 to 4500 cal yr BP (Heiri et al., 2015; Tóth et al., 2015; Hájková et al., 2016). Climate simulations are consistent with this pattern of mid Holocene cooling, but also marked precipitation and soil moisture increases (Feurdean et al., 2013). Palaeoecological reconstructions show that significant forest expansion occurred in response to cool and moist conditions in Central Eastern Europe (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al., 2015; Novenko et al., 2016; Pokorný et al., 2015; Jamrichová et al., 2017; Moskal del Hoyo et al., 2018). Therefore, both proxy and modelled palaeoclimatic and palaeoecological evidence from the lowlands of Central Eastern Europe clearly show that grasslands were most extensive during the warm and dry climatic conditions, with prolonged droughts, of the early Holocene (11,700–9000 cal yr BP) and became restricted under wetter conditions during the mid Holocene (9000–4500 cal yr BP). This illustrates the stronger competitive advantage of grasslands over trees when resources are limited i.e., lower moisture availability and prolonged droughts.

Table 2

Fossil pollen, plant macrofossil and charcoal evidence for the presence of various types of grasslands during the early and mid Holocene. Note: on the basis of pollen analysis differentiation between primary grassland and semi-natural grassland is not always possible.

| Location | Taxa | Period | References |
|----------------|--|--------------------|---|
| Romania | <i>Artemisia</i> , <i>Aster</i> -type, Caryophyllaceae undiff., Compositae Cichorioideae, <i>Centaurea</i> , Chenopodiaceae, <i>Helianthemum</i> , <i>Filipendula</i> , <i>Potentilla</i> , Poaceae, <i>Plantago lanceolata</i> , <i>Plantago major</i> / <i>P. media</i> , <i>Rumex acetosa</i> , <i>Thalictrum</i> , <i>Chenopodium</i> , <i>Suaeda maritima</i> , <i>Festuca</i> , <i>Lycopus</i> , <i>Thymus</i> , Leguminosae undiff. | Holocene | Feurdean et al., 2015 |
| Hungary | <i>Artemisia</i> , <i>Achillea</i> , <i>Ajuga</i> , <i>Adonis</i> , <i>Astragalus</i> , <i>Allium</i> , <i>Aster</i> -type, Poaceae, <i>Centaurea</i> , <i>Filipendula</i> , <i>Festuca</i> , <i>Euphorbia</i> , Caryophyllaceae undiff., <i>Gagea</i> , Chenopodiaceae, Compositae Cichorioideae, <i>Dianthus</i> -type, <i>Genista</i> , <i>Helianthemum</i> , <i>Hypericum</i> , <i>Inula</i> , Leguminosae undiff., <i>Lotus</i> -type, <i>Plantago lanceolata</i> , <i>Plantago major</i> / <i>P. media</i> , <i>Potentilla</i> , <i>Trifolium</i> , <i>Rumex acetosa</i> , <i>Teucrium</i> , <i>Thymus</i> , <i>Thalictrum</i> , <i>Verbascum</i> , <i>Sanguisorba</i> | Holocene | Magyari et al., 2010 |
| Hungary | <i>Chenopodium album</i> , <i>Echinochloa crus-galli</i> , <i>Fallopia convolvulus</i> , <i>Galium spurium</i> , <i>Melandrium album</i> , <i>Plantago lanceolata</i> , <i>Polycneum arvense</i> , <i>Polygonum aviculare</i> , <i>Polygonum mite</i> , <i>Polygonum minus</i> , <i>Rumex acetosa</i> , <i>Setaria pumila</i> , <i>Setaria viridis</i> , <i>Bromus</i> sp., <i>Chenopodium</i> sp., <i>Galium</i> , <i>Ononis</i> sp., <i>Polygonum</i> sp., <i>Rumex</i> sp., <i>Stipa</i> sp., <i>Trifolium</i> sp., <i>Vicia</i> sp., Fabaceae, Poaceae, Polygonaceae, Caryophyllaceae | Neolithic | Moskal del Hoyo, 2013 |
| Poland (S) | <i>Artemisia</i> , <i>Stipa</i> sp., <i>Knautia arvensis</i> , <i>Hypericum</i> , <i>Plantago media</i> , <i>P. lanceolata</i> , <i>Filipendula</i> , <i>Aster</i> -type, Compositae Cichorioideae, Poaceae, Chenopodiaceae | Mid Holocene | Moskal del Hoyo et al., 2018 |
| Czech Republic | <i>Artemisia</i> , <i>Achillea</i> , <i>Ajuga</i> , <i>Astragalus</i> , <i>Filipendula</i> , Chenopodiaceae, <i>Centaurea</i> , Caryophyllaceae undiff., Compositae Cichorioideae, <i>Genista</i> , <i>Filipendula</i> , <i>Helianthemum</i> , <i>Hypericum</i> , <i>Inula</i> -type, <i>Plantago lanceolata</i> , <i>P. media</i> , Poaceae, <i>Potentilla</i> -type, <i>Ranunculus acris</i> -type, Rubiaceae, <i>Rumex acetosa</i> , <i>Teucrium</i> , <i>Thymus</i> , <i>Thalictrum</i> , <i>Verbascum</i> | Holocene | Kuneš et al., 2015 Jamrichová et al., 2017 Hájek et al., 2016 |
| Austria | <i>Poa pratensis/trivialis</i> , <i>Festuca ovina/rubra</i> , <i>Brachypodium pinnatum</i> , <i>Anthoxanthum odoratum</i> , <i>Stipa pennata</i> | Neolithic | Körber-Grohne, 1990 |
| Germany (S) | <i>Alchemilla vulgaris</i> , <i>Asperula cynanchica</i> , <i>Bupleurum falcatum</i> , <i>Carex muricata</i> , <i>Centaurea</i> , <i>Daucus carota</i> , <i>Euphrasia</i> , <i>Phleum pratense</i> , <i>Poa annua</i> , <i>Polygonum aviculare</i> , <i>Stipa</i> sp., <i>Stipa pennata</i> , <i>Rumex acetosella</i> , <i>Stellaria graminea</i> , <i>Trifolium campestre</i> , <i>Galium</i> cf. <i>verum</i> , <i>Galium molugo</i> , <i>Urtica dioica</i> , <i>Teucrium chamaedrys</i> , <i>Chenopodium</i> spp., <i>Veronica arvensis</i> , <i>Plantago media</i> | Neolithic | Kreuz et al., 2005, Kreuz, 2008 Kreuz and Schäfer, 2011 |
| Germany (NW) | <i>Achillea ptarmica</i> , <i>Angelica sylvestris</i> , <i>Anthriscus sylvestris</i> , <i>Artemisia</i> cf. <i>campestris</i> , <i>Crepis biennis</i> , <i>Chaerophyllum hirsutum</i> , <i>Dianthus</i> spp., <i>Empetrum nigrum</i> , <i>Euphorbia cyparissias</i> , <i>Festuca</i> cf. <i>pratensis</i> , <i>Festuca rubra</i> , <i>Filipendula ulmaria</i> , <i>Galium mollugo</i> , <i>Heracleum sphondylium</i> , <i>Hypochaeris radicata</i> , <i>Juncus</i> cf. <i>effusus</i> , <i>Knautia arvensis</i> , <i>Lysimachia vulgaris</i> , <i>Laserpitium prutenicum</i> , <i>Poa pratensis/angustifolia</i> , <i>Polemonium coeruleum</i> , <i>Scabiosa columbaria</i> , <i>Plantago lanceolata</i> , <i>Potentilla tabernaemontani</i> , <i>Ranunculus acris</i> , <i>Rumex acetosa</i> , <i>Rumex tenuifolius</i> , <i>Sanguisorba officinalis</i> , <i>Scabiosa</i> aff. <i>columbaria</i> , <i>Silene vulgaris</i> , <i>Thalictrum flavum</i> , <i>Valeriana officinalis</i> , <i>Valeriana procurrens</i> , <i>Viola canina</i> | Preboreal & Boreal | Knörzer, 1996 |
| Germany (NW) | <i>Achillea millefolium</i> , <i>Leontodon autumnalis</i> , <i>Agrostis tenuis</i> , <i>Melandrium rubrum</i> , <i>Phleum nodosum</i> , <i>Poa</i> cf. <i>pratensis</i> , <i>Artemisia</i> cf. <i>campestris</i> , <i>Poa</i> cf. <i>trivialis</i> , <i>Polygonum bistorta</i> , <i>Potentilla argentea</i> , <i>Carex ovalis</i> , <i>Prunella vulgaris</i> , <i>Centaurea</i> cf. <i>nigra</i> , <i>Ranunculus repens</i> , <i>Cerastium</i> cf. <i>semidecandrum</i> , <i>Rumex tenuifolius</i> , <i>Chrysanthemum leucanthemum</i> , <i>Deschampsia caespitosa</i> , <i>Selinum carvifolium</i> , <i>Festuca rubra</i> , <i>Silene silaus</i> , <i>Heracleum sphondylium</i> , <i>Stachys recta</i> , <i>Hieracium pilosella</i> , <i>Trifolium arvense</i> , <i>Hypericum</i> cf. <i>maculatum</i> , <i>Trifolium dubium</i> , <i>Hypericum tetrapterum</i> , <i>Valerianella dentata</i> , <i>Juncus bufonius/conglomeratus</i> , <i>Veronica</i> cf. <i>arvensis</i> , <i>Trifolium repens</i> , <i>Juncus</i> cf. <i>effusus</i> , <i>Viola tricolor</i> | Neolithic | Knörzer, 1996 |

4.2. Fire

The role of fire as one of the main drivers of the rise in grassy ecosystem during the Miocene has been advocated (Strömberg, 2011) and confirmed by fossil records from C₄ dominated grasslands in Africa (Hoetzel et al., 2013). This is not surprising as dominant grassland species have fine fuels with rapid curing and fast regrowth rates as well as perennating buds near or below the soil surface. These adaptations ensure regeneration after disturbances that damage the above-ground parts of the plant (He and Lamont, 2018). Thus, whilst grass and herbs can withstand frequent fire, this shift in fire regime may have harmed previously dominant tree species adapted to infrequent fire (He and Lamont, 2018). Although, short-term, field-based burning experiments in Hungary found conflicting results about the effect of fire on grassland biodiversity (Valkó et al., 2014, 2018b), controlled laboratory and small-scale field experiments examining the effect of fire on seeds found a predominantly negative effect of fire on seed germination in grassland species, however, some positive effects (Fabaceae) also emerged (Ruprecht et al., 2013, 2015). Disturbances by fire have recently been

considered essential for increased grassland competitive advantage over trees during the Holocene in Central Eastern Europe (Magyari et al., 2010; Feurdean et al., 2015). For example, a positive effect of frequent fires on the competitive advantage of grasses over trees and, by this means, on the extent of grassland in Transylvania, Romania, has been inferred from sedimentary charcoal particles and pollen (Feurdean et al., 2013). On the contrary, the decline in fire frequency during the mid Holocene has been shown to be detrimental for grassland extension. Taken together, neo- and palaeoecological evidence indicate that fire may have had a more important role in the shifts between forest and grassland, and in grassland maintenance, than previously thought. Exploring to what extent temperate grasslands are associated with frequent fires and which grassland species/communities are most resilient or benefit most from fire could be useful for the enhancement of management practices, i.e., preventing excessive dominance by competitor grass species as well as succession towards shrublands and forests.

4.3. Herbivores

Large herbivorous mammals influence the physiology and growth of plants and are considered ecological keystones in maintaining tree–grass coexistence (Crawley, 1983; Sankaran et al., 2005). Released from megaherbivore pressure and with a change in climate at the Pleistocene–Holocene boundary, European lowlands witnessed substantial forest regeneration and a reduction in vegetation openness (Vera, 2000; Svenning, 2002). Megaherbivore extinction may also have had a cascading effect on the population size and diversity of small mammals dependent on vegetation openness and indirectly on the fire regime (Gill, 2014). However, comparatively, little attention has been given to the effect of the declining population size or extinction of wild herbivores, or the subsequent role of livestock, on landscape structure during the mid to late Holocene. We know from palaeontological and archaeozoological records in the Carpathian Basin that several large herbivores i.e., *Alces alces* (Eurasian Elk), *Bison bonasus* (European Bison), *Dama dama* (Eurasian Fallow Deer), *Equus ferus* subsp. *gmelini* (Wild Horse) and *Equus hemionus* (Asiatic Wild Ass), became discontinuously present from the mid Holocene, i.e., 8000 cal yr BP and that many became extinct by 4000 cal yr BP (Németh et al., 2017; Bejenaru et al., 2018). In contrast, livestock numbers increased from 6500 cal yr BP (Schumacher et al., 2016). Domestic livestock could prevent forest encroachment in the absence or with a low density of wild herbivores (Bruun and Fritzboøger, 2002; Cosyns et al., 2005), however, their movement is limited by agricultural practices. Combined fossil records of fauna, pollen and coprophilous fungi that reproduce exclusively on animal dung (*Sporormiella* spp., *Sordaria* spp., *Podospira* spp.) can provide means of assessing the effects of herbivores on grassland dynamics and also the timing of the shift in influence from grazing by wild herbivores to livestock grazing (Gill et al., 2009). Such records are still scant in Europe, but the existing studies generally show the increasing effects of grazing by domestic livestock from 6500 cal yr BP (Schumacher et al., 2016). Understanding the responses of grasslands to different grazing animals (body size, grazing intensity and height, foraging strategy and forage selectivity) will be essential in the development of future grassland management strategies as various forms of livestock grazing have been proposed to simulate the effects of grazing and browsing by wild herbivores (Poschlod and Wallis de Vries, 2012; Bakker et al., 2006; Tóth et al., 2016; Poschlod, 2017).

4.4. Early human impact counteracted the encroachment of forest onto primary grasslands

As the increase in forest cover from 8000 cal yr BP coincided with the spread of Neolithic culture across South Eastern Europe (Bogaard, 2004; Kreuz, 2008), a critical question in respect to grassland extent is whether anthropogenic impacts could have counteracted the climate-driven development of a closed forest (Pokorný et al., 2015). Archaeological datasets from this part of Europe indicate that Neolithic settlements tended to be established in open landscapes and that field sizes were small (Moskal del Hoyo, 2013; Chapman, 2017; Marinova and Ntinou, 2017). As people first settled in naturally open landscapes, this tendency could explain the apparent lack of major deforestation at this time in the pollen records from Central Eastern Europe (Fig. 2). Fire activity was naturally high during the early Holocene (Magyari et al., 2010; Feurdean et al., 2013) and humans may have taken advantage of wildfires to extend their agro-pastoral activities into freshly burned habitats. In agreement with Pokorný et al. (2015) we hypothesise that early anthropogenic land management may have slowed, or partially arrested, the development of closed forest favoured by the wetter climatic conditions of the mid Holocene at locations with low biomass productivity, contributing to the maintenance of landscape openness.

4.5. Semi-natural grasslands replaced forests: when and how?

Individual pollen records, as well as large-scale quantitative vegetation reconstructions from Central Eastern Europe, show that the level of anthropogenic impact on forest remained low until about 6000–5000 cal yr BP (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al., 2015; Jamrichová et al., 2017; Fig. 2). Modelled vegetation and land use (arable and pasture cover) changes across Europe suggest that open areas expanded gradually from previously cleared forest after ca. 6000 cal yr BP (Kaplan et al., 2017). A noticeable increase in the abundance and richness of grassland with a decline in total forest cover, but increase in *Quercus*, a tree taxon typical of woodland and woody pasture in Central Eastern Europe occurred from 4700 to 3500 cal yr BP onwards (Jamrichová et al., 2017). This demonstrates a growing anthropogenic role in the extension of grasslands and the formation of open woodlands. These grasslands belong to the so-called semi-natural grasslands that developed from forests and are maintained by land management (Pärtel et al., 2005; Pereira et al., 2017). Technological advances in agriculture and the expansion of urban centres and farms from the Late Bronze Age and Iron Age (3500 cal yr BP) have led to both an extension and intensification of the land use in Central Europe (Poschlod, 2015; Rösch and Lechterbeck, 2016). It is therefore not surprising that from this time onwards, the richness and extent of grassland has been found to correlate closely with prehistoric settlement density, land management and socio-political trends (Poschlod and Wallis de Vries, 2012; Pärtel et al., 2005; Hájková et al., 2011; Hejman et al., 2013; Poschlod, 2017; Feurdean et al., 2017). Later on i.e., from the 15th to 20th centuries, grassland expansion is strongly linked to sheep flock migration. Livestock acted as dispersal vectors and their mobility may be one of the reasons that ancient and older semi-natural grasslands have similar species diversity (Poschlod and Wallis de Vries, 2012; Molnár et al., 2012; Poschlod, 2017). The sowing of hayseed and mowing may also have promoted grassland expansion in many parts of Europe (Babai and Molnár, 2014). In summary, semi-natural grasslands expanded into formerly forested sites and have subsequently been maintained by a variety of land management practices including grazing, burning and mowing.

5. A new framework for Holocene grassland persistence; conservation consequences

We provide a new framework distinguishing three types of biodiversity-rich grasslands in Central Eastern Europe. These are: primary grasslands on skeletal and other poor soils (primary grasslands I), ancient grasslands on potential forest area (primary grasslands II), and semi-natural grasslands replacing forests (Fig. 3; Table 1). We have identified the reasons for the continuous presence of primary grasslands during the Holocene including natural i.e., climate conditions and soils (primary I), as well as climate and disturbance factors e.g., fire and grazing (primary grasslands II). Neolithic people may have first settled in naturally open areas such as grasslands or grassland-woodland mosaics arresting the development of a full forest cover when the climate became wetter (mid Holocene), indirectly favouring the preservation and expansion of grasslands. The intensification of human impact from 4700 to 3500 cal yr BP onwards subsequently lead to considerable extension of semi-natural grassland on formerly forested sites. A succession from grassland to forest after the cessation of land management (e.g., grazing or burning) is not necessarily evidence against the primary or ancient aspect of grasslands, but may indicate the lack of disturbances. Livestock grazing in the late Holocene replaced ancient grazing by megaherbivores that prevailed until the early Holocene and that by large herbivores throughout the mid Holocene.

Our findings also reveal misconceptions about the origin of Central Eastern European grasslands and open canopy woodlands. The concept of a previously continuous, closed forest in extant grassland-rich landscapes where climatic conditions are favourable for forest fails to hold

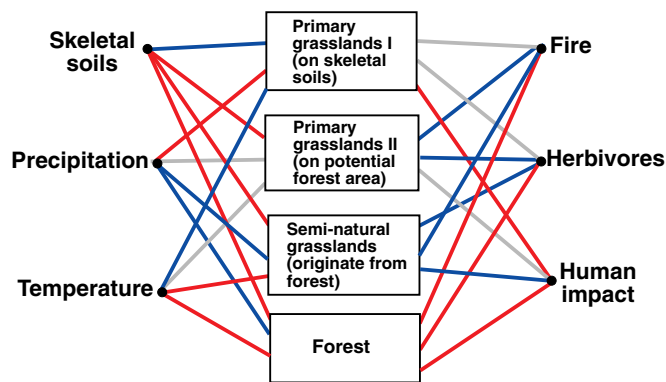


Fig. 3. The effect of climate, soils and disturbances by fire, herbivores and humans on the three types of grasslands and forest. Blue line denotes a positive effect, red line a negative effect and grey both effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

true, as grasslands are likely to have been continuously present throughout the Holocene. The long-term persistence of grasslands at these locations is probably an important reason for one of the highest small-scale species richness, many endemic, worldwide in these habitats. Such species-rich plant communities can require millennia to develop and only well-connected grassland patches can support genetically diverse plant populations. These findings challenge the commonly held view that conservation activities should primarily focus on the protection of forests in many areas of Central Eastern Europe.

Anthropogenic impacts tend to focus on forest clearance, but this perspective paper highlights that conservationists and land managers need to carefully consider that, in many cases, it is not primary forests that hold the highest biodiversity. Further, human-made, or managed environments, such as extensively managed grasslands, are long-term landscape features, contain unique plant and animal communities, and provide important ecosystems services. Our findings support the recent wider acceptance of the notion that people and nature should not be separated in the societal discourse of environmental science (Mace, 2014). Finally, we advocate the need for a more detailed understanding of the role of disturbances in grassland-forest dynamics, to avoid the overly simplistic assumption that sparse tree cover is evidence of past deforestation. Fossil records provide such data and the routine incorporation of palaeoecological investigations into environmental management is a key step in developing science-based evidence for the conservation of the biodiversity of grasslands. Thus, our regional case study supports the advocacy of Willis et al. (2008), Barnosky et al. (2017) and Whitlock et al. (2018) for merging palaeobiology and conservation biology as well as an appreciation of the dynamic history of species and ecosystems, including the role of humans.

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Conflict of interest

There is no conflict of interest with any other people or organisations.

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